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Estimating zooplankton biomass from dry weights of groups of individual organisms

Estimation de la biomasse du zooplancton à partir des poids secs de groupes d'organismes individuels

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Abstract

Mesozooplankton biomass is measured for samples collected in the AZMP (Atlantic Zone Monitoring Program) either as wet weight, after draining the entire sample, or as dry weight for one half of the sample, after splitting, filtering on to pre-weighed filters and drying at 60°C for 24 h. Mesozooplankton samples are often contaminated with large amounts of phytoplankton whose biomass will be included in the mesozooplankton sample wet and dry weights determined using the AZMP protocol. Between 1998 and 2001, another set of mesozooplankton samples (Head and Harris samples) were collected during AZMP cruises on the Scotian Shelf in the 0-100 m depth range. These were analysed using a different protocol. Counts and dry weights were determined for mesozooplankton, by picking individual organisms and placing them into a series of groups, according to stage and species, genus, or some broader taxonomic group. The groups were dried (60°C, 1-4 days) and average individual dry weights were determined. The total dry weight biomass was calculated by summing the dry weights of the organisms in each of the component groups. This method excludes the contribution of phytoplankton. Amongst the groups for which dry weights were measured were each of the developmental stages of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* and groups of mixed stages of *Oithona* spp. and *Pseudocalanus* spp.. Average individual dry weights were lower in fall than in spring for all of the *C. finmarchicus* stages and *Oithona* spp.. The same trend was apparent for the other *Calanus* species, although in the fall only a few stages were encountered and these at only a few stations. Seasonal average individual dry weights were generally similar in eastern and western regions of the Scotian Shelf. Seasonal average individual dry weights and abundance estimates were used to calculate the sum of the dry weights for only these five mesozooplankton species/genera for the Head and Harris samples. In spring these accounted for over 60% of the total mesozooplankton in most cases and often over 70%. The same individual dry weight averages were applied to the abundance data for AZMP samples from the Scotian Shelf. The summed dry weights of these five species/genera were sometimes less than and sometimes greater than the measured dry weights. Most of the measurements were within a factor of two of the calculated weights, however. The discrepancies may be partly due to the splitting, sub-sampling and counting procedures used in the AZMP protocol. Combining individual dry weight and abundance data allows estimation of the contributions of these important groups to the total mesozooplankton biomass. Average individual dry weights of late state *Calanus* spp. on the Labrador and Newfoundland Shelves were similar to Scotian Shelf spring values in May and early June but *ca.* 30% higher in late June and July. Other groups also showed some differences. Thus, average seasonal individual dry weights values derived from one region should not be used for other regions without validation.

Résumé

La biomasse du mésozooplancton des échantillons recueillis dans le cadre du PMZA (Programme de monitorage de la zone atlantique) est mesurée de deux façons : en poids humide, après drainage de tout l'échantillon, ou en poids sec déterminé pour la moitié de l'échantillon, après fractionnement, filtration sur des filtres pré-pesés et séchage à 60 °C durant 24 h. Les échantillons de mésozooplancton sont souvent contaminés par de grandes quantités de phytoplancton dont la biomasse est comprise dans les poids humides et les poids secs de mésozooplancton déterminés selon le protocole du PMZA. Entre 1998 et 2001, une autre série d'échantillons de mésozooplankton (échantillons Head et Harris) ont été obtenus entre 0 et 100 m de profondeur lors des croisières du PMZA sur le plateau néo-écossais. Ces échantillons ont été analysés selon un autre protocole. En effet, les organismes constituant le mésozooplancton ont été prélevés individuellement, dénombrés et placés dans des groupes de mêmes espèce et stade, de même genre ou d'un même taxon plus général. Les groupes ont été séchés (à 60 °C de un à quatre jours), et on a déterminé le poids sec moyen individuel pour chaque groupe. La biomasse totale en poids sec a été calculée en faisant la somme des poids secs des organismes de tous les groupes. Cette méthode évite d'inclure le poids du phytoplancton. Les groupes dont on a calculé le poids sec comprenaient chacun des stades de développement de *Calanus finmarchicus*, de *C. glacialis* et de *C. hyperboreus*, ainsi que *Oithona* spp. et *Pseudocalanus* spp., tous stades confondus. Les poids secs individuels moyens de *Oithona* spp. et de tous les stades de *C. finmarchicus* étaient moins élevés à l'automne qu'au printemps. Les autres espèces de *Calanus* semblaient présenter la même tendance, mais, à l'automne, seuls quelques stades n'ont été observés qu'à quelques-unes des stations. En général, les moyennes saisonnières des poids secs individuels étaient semblables dans les parties est et ouest du plateau néo-écossais. Les moyennes saisonnières des poids secs individuels et des données d'abondance ont servi à calculer la somme des poids secs de ces cinq espèces ou genres de mésozooplancton pour les échantillons Head et Harris. Au printemps, ces organismes représentaient plus de 60 % de l'ensemble du mésozooplancton dans la plupart des cas et souvent plus de 70 %. Les mêmes moyennes de poids secs individuels ont été appliquées aux données d'abondance pour les échantillons prélevés sur le plateau néo-écossais dans le cadre du PMZA. Les sommes des poids secs de ces cinq espèces et genres étaient parfois inférieures et parfois supérieures aux poids secs mesurés, mais la plupart des mesures ne différaient pas des poids calculés par un facteur de plus de deux. Les écarts seraient attribuables en partie aux procédures de fractionnement, de sous-échantillonnage et de dénombrement du protocole du PMZA. La combinaison des données de poids secs individuels et des données d'abondance permet d'estimer les contributions de ces groupes importants à la biomasse totale du mésozooplancton. À la fin de juin et en juillet, les poids secs individuels moyens de *Calanus* spp. au dernier stade étaient d'environ 30 % plus élevés sur les plateaux du Labrador et de Terre-Neuve que sur le plateau néo-écossais, alors qu'ils étaient semblables en mai et au début de juin. D'autres groupes ont également présenté des différences à cet égard. Ainsi, les moyennes saisonnières des poids secs individuels dans une région ne devraient pas être utilisées pour d'autres régions sans validation.

Introduction

Sampling in the AZMP (Atlantic Zone Monitoring Program) includes the collection of mesozooplankton in vertical ring net hauls (200 μm mesh) at time-series coastal stations at bi-weekly intervals and at stations along transects across the Scotian Shelf and Cabot Strait in spring and fall. As indices of mesozooplankton biomass, the AZMP analysis protocol includes the determination of sample wet and dry weights (Mitchell *et al.* 2002). Wet weights are measured for whole samples filtered on to pre-weighed filters. After this, the zooplankton are returned to their original seawater/formalin preservation medium and the samples are split into two halves. One half is sub-sampled and used for identification and enumeration of individual organisms. The other is filtered on to one or more pre-weighed filters and dried at 60°C for at least 24 h to give the total sample dry weight. One of the problems with these methods of estimating zooplankton biomass is that at high *in situ* chlorophyll concentrations, large amounts of phytoplankton are collected in the 200 μm mesh nets, along with the zooplankton. During bloom conditions, such as are encountered on the Scotian Shelf in spring, the phytoplankton in the preserved samples sometimes occupy a larger settled volume than do the zooplankton. In such cases wet and dry zooplankton biomass will be overestimated.

A second set of mesozooplankton samples (Head and Harris samples) was collected, in addition to the AZMP samples, during each of the cruises to the Scotian Shelf between 1998 and 2001. Mesozooplankton samples were also collected at stations on the Newfoundland Shelf and Labrador Shelf over Hamilton Bank. Zooplankton abundance and dry weight biomass was determined for these samples, but the methodology that was used was different from the AZMP protocol. It involved the counting, picking and weighing groups of organisms from each sample, and reconstructing the dry weights of the samples from the dry weights of the picked groups. In this method, no phytoplankton were included in the total dry weight biomass estimates. As well as allowing for the estimation of total zooplankton biomass, this method also enabled estimation of average individual dry weights for each of the copepodite and adult stages of *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* whenever they were present. Average individual weights of groups of mixed stages for *Oithona* spp. were determined at every station, since they are ubiquitous in their distribution.

In this paper, we will describe in detail the method used to determine the abundance and biomass of mesozooplankton for the Head and Harris samples. Next, we will examine the seasonal and regional variations in individual dry weights of the copepodite and adults stages of the three species of *Calanus* and the average individual dry weights of mixed stages of *Oithona* spp. and *Pseudocalanus* spp.. We will then apply appropriate average individual dry weights for each of these groups to the abundance estimates for the Head and Harris samples from the Scotian Shelf. Their sum will then be compared with the dry weights of total copepods and total mesozooplankton, which were calculated using the individual dry weights measured for each of the groups at each station.

We will then use data from the Biochem database to compare the sum of the dry weights calculated from abundance data and individual weights for the *Calanus* spp. stages and *Oithona* and *Pseudocalanus* stage assemblages with the wet and dry sample weights for the AZMP samples collected on the Scotian Shelf between 1998 and 2003. Finally, we will compare individual dry weights measured on the Scotian Shelf with those determined for organisms collected on the Newfoundland Shelf, over Hamilton Bank and in the adjacent slope waters.

Methods

Analysis of mesozooplankton samples by the Harris method.

For the Head and Harris samples, in each case a 10% aliquot of the original sample is removed and the remainder is archived. The aliquot is strained and put into filtered seawater prior to further analysis. A small sub-sample (*e.g.* 1-5%) of the aliquot is taken for the identification and enumeration of the small abundant copepods (*e.g. Oithona* spp. and *Pseudocalanus* spp.). As they are counted, individual copepods are picked out and put into Petrie dishes in groups. A mixture of *Oithona* stages and species always constitutes one group, but other small copepods are sometimes separated by species (if abundant) or put into a group called "small copepods" if unidentified or rare. Roughly 100 organisms are required to give an accurate estimate of dry weight for the groups containing small copepods. For the larger organisms, additional larger sub-samples of the original aliquot are required to get a valid count of the number of organisms and enough material for accurate dry weight determination. The copepodite and adult stages of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* are put into separate groups (up to 21 different groups) and for these the aim is to count and pick 25 individuals of each stage for each species. The other groups are not identical for all stations, but depend on the composition of the sample. As with the small copepods, the groups of larger organisms may contain mixtures of stages for a given species, or be comprised of, for example, "large copepods" or "chaetognaths" or "jellies". Occasionally a group might contain a single large pteropod or euphausiid, since all zooplankton in the aliquot are accounted for amongst the groups. The proportion of the initial aliquot that is sampled to get valid counts and dry weights for each of the groups is recorded. This might be as low as 1% for the small copepods, but for some groups (*e.g.* fish larvae) the entire aliquot is processed. After processing is finished, the groups are blotted dry on sharkskin filters, put on to small Teflon plates, dried at 60°C for 1-4 days, scraped off and weighed. The dry weight of the aliquot, and hence of the original sample, is reconstructed by taking the dry weights per individual for each of the groups and by multiplying these by their abundance. Dry weight biomass determined by this method includes only zooplankton.

Sample and data sources

Head and Harris samples
Calanus groups
Individual dry weights were determined from samples collected in 0-100 m, or 0-bottom, vertical net hauls on the Scotian Shelf (Spring: April 1998-2000, May 2001; Fall: October 1998), on the Newfoundland Shelf (Spring: May 1997, Summer: July 1995) and on the Labrador Shelf over Hamilton Bank and in the adjacent Labrador Slope waters (Spring: May/early June 1996, 1997, 2000, Summer: late June/July 1995, 1998, 1999). On the Scotian Shelf the Browns Bank, Roseway, Halifax and Cabot Strait Lines were sampled on a regular basis (Fig. 1). Additional stations (not shown) were sampled on some cruises.

Oithona
Individual dry weights for mixed stages of *Oithona* spp. were determined for the same set of samples as were used for the estimation of those of the *Calanus* groups, except that no *Oithona* were weighed for samples for the 2001 Scotian Shelf spring cruise or for the Newfoundland Shelf spring cruise.

Pseudocalanus
Individual dry weights for *Pseudocalanus* spp. were determined or samples collected on the Scotian Shelf in April 1995 and May/June 1996, and for the same stations on the Newfoundland Shelf, over Hamilton Bank and the adjacent Labrador Slope waters as for the other groups, except none were weighed for the Newfoundland Shelf spring cruise or the Labrador Slope waters in summer.

Abundance data were also available for all of these cruises, as were estimates of "Total copepods" and "Total mesozooplankton" dry weight, as determined by the Harris method.

AZMP data
Data on the abundance of the stages of the three species of *Calanus*, together with information on the abundance of the sum all stages of *Oithona* and *Pseudocalanus* spp. were extracted from the Biochem database, as were data on sample wet and dry weights. Only data from the Scotian Shelf were used, which included data from the time series station (HL2) as well as data from spring and fall cruises. Wet and dry weights were not determined for all samples. For some samples there was only a wet weight, for some, only a dry weight and for some, both.

Results

The frequency distributions of individual dry weights for *C. finmarchicus* and *C. hyperboreus* females, stage Vs and stage IIIs are shown as examples of the patterns that were typical for *Calanus* spp., *Oithona* and *Pseudocalanus* groups for

data for all five cruises on the Scotian Shelf (Fig. 2). For most stations most average individual dry weights varied by a factor of between 2 and 4.

In order to see the extent to which average individual dry weights varied between cruises for the *Calanus* groups, cruise averages were compared (Fig. 3, Tables 1-3). Individual dry weights of all stages of *C. finmarchicus* were much lower in fall than in spring. Individual dry weights also varied amongst the four spring cruises, and some of the differences were significant, but they generally not very large. For the few stages of *C. glacialis* and *C. hyperboreus* that were present in the fall, individual dry weights were generally lower. For these species, spring values did not vary consistently over all stages between cruises, and the variations were not large. The same pattern of higher dry weights in spring than in fall was also observed for *Oithona*, but seasonal differences could not be determined for *Pseudocalanus*, since no dry weight data were available for the fall.

Variations in average individual dry weights between eastern (Cabot Strait and Louisbourg Lines) and western (Halifax and Browns Bank Lines) lines were examined for samples using spring and fall averages (Fig. 5). For *C. finmarchicus* the regional differences were very small. For *C. glacialis* stages I-IV and *C. hyperboreus* stages I-III, spring averages were generally higher in the east than in the west. The later stages did not show regional differences in spring, and in fall there were too few data to draw any conclusions.

Dry weight biomass for *Calanus* spp. stages, *Oithona* and *Pseudocalanus* spp. were calculated for the Head and Harris samples using seasonal average individual dry weights and abundances for stations sampled during spring (1998, 1999, 2000) and fall (1998) (Fig. 5). The total varied between <0.1 g m^{-2} and close to 10 g m^{-2}. Values were always low on Banquereau Bank (LL6) and beyond the shelf-break in fall (BBL6 and 7, HL6 and 7, LL7 and 8). In spring, there was a gradient in biomass from west to east, with Cabot Strait always showing the highest values. On the two western lines (Browns Bank and Halifax Lines) *C. finmarchicus* generally contributed a large proportion of the total biomass. By contrast, on the two eastern lines, *C. hyperboreus* was most important. In the fall biomass was lower than in spring, except at one station in Cabot Strait, and *C. finmarchicus* was dominant more-or-less everywhere. *Oithona* and *Pseudocalanus* together made a minor contribution to the total biomass, with their highest contribution being recorded in the west in spring 1998.

Estimated dry weights, shown on the Y-axis in Fig. 6, are the dry weights calculated by the Harris method, *i.e.* the individual weights of the *Calanus* spp. stages and *Oithona* and *Pseudocalanus*, measured at each station, were used to calculate their dry weights. In the upper panel these were summed with the dry weights of the other copepods in the samples. In the lower panel all other forms (*e.g.* euphausiids, chaetognaths, pteropods *etc.*) were included. The corresponding summed dry weights of the *Calanus*, *Oithona* and *Pseudocalanus* (*C* + *O* + *P*) groups, calculated using the seasonal average dry weights, are shown

on the X-axis. These accounted for *ca.* 90% of the variance in total copepod dry weight in spring and *ca.* 74% in fall. For the total mesozooplankton dry weight, these groups accounted for *ca.* 82% of the variance in spring and *ca.* 64% in the fall. For the AZMP data, which contained a few HL2 values for all months of the year, the January-July period was considered to be spring, and August-December, fall. The dry weights summed for the *C* + *O* + *P* groups only accounted for *ca.* 21% of the variance in measured dry weight and *ca.* 46% of that in wet weight in spring (Fig. 7). In the fall, they accounted for *ca.* 77% of the variance in dry weight, but only *ca.* 42% of variance in wet weight.

Over 60% of the stations on the Scotian Shelf (spring and fall) showed a ratio of Head and Harris total mesozooplankton dry weight: *C* + *O* + *P* dry weight of between 1 and 2 (Fig. 8, upper panel). At 51% of the stations the ratio was between 1 and 1.6, and at these stations *C* + *O* + *P* accounted for >60% of the total mesozooplankton dry weight. For the AZMP data *ca.* 70% of the stations had a ratio of measured sample dry weight: *C* + *O* + *P* dry weight of between 0.5 and 2 (Fig. 8, lower panel). Measured sample wet weight: *C* + *O* + *P* dry weight ratios were mostly between 5 and 10.

The Harris sample analysis method was also used for samples collected on the Newfoundland Shelf in May/June 1997 (spring) and July 1995 (summer), over Hamilton Bank and in the Labrador Slope waters adjacent to Hamilton Bank in May/June 1996, 1997 and 2000 and July 1995, 1998 and 1999. Female and Stage V *C. finmarchicus* were smaller in spring than in summer over Hamilton Bank and in the Labrador Slope waters, while on the Newfoundland Shelf stage Vs were the same size in spring and summer (Fig. 9, Table 4). The younger *C. finmarchicus* stages were larger in spring than in summer on the Newfoundland Shelf and in the Labrador Slope waters, but larger in summer than in spring over Hamilton Bank. For both *C. glacialis* and *C. hyperboreus*, females and Stage Vs over Hamilton Bank and in the Labrador Slope waters were larger in summer than in spring, but on the Newfoundland Shelf they were either slightly larger in summer (females) or the same size (Stage Vs) in spring and summer (Fig. 9, Tables 5 and 6). For *C. glacialis*, patterns of size variation were inconsistent for the younger stages, although the lowest weights at stage always occurred on the Newfoundland Shelf in summer. Stages I-IV of *C. hyperboreus* also showed no consistent patterns of size variation. Weights at stage for all three *Calanus* spp. on the Scotian Shelf were generally within the range of values measured in the three other regions. Average dry weights of mixed stages of *Oithona* were highest in the Labrador Slope waters in spring, but otherwise quite similar and similar to values on the Scotian Shelf in spring (Table 8). The average individual dry weights of mixed stages of *Pseudocalanus* on Hamilton Bank and in the Labrador Slope waters in spring were three times higher than spring values on the Scotian Shelf. Summer values on the Newfoundland Shelf were close to spring values on the Scotian Shelf, while summer values on Hamilton Bank were a little higher.

Discussion

Dry weights at stage of individual copepods vary according to the environmental conditions they experience during development. If food is readily available, growth and development rates increase with temperature and stage duration decreases (McLaren 1963, Corkett *et al.* 1986). Under these conditions, weights at stage decrease with increasing temperature. Thus, for example, Stage V *C. finmarchicus* reared with excess of food at 12°C had 14% less nitrogen and 15% less carbon than those reared at 4°C (Campbell *et al.* 2001). At a constant temperature, a lack of food reduces growth and development rates, lengthens stage durations and leads to reduced weights at stage. Thus, for example, Stage V *C. finmarchicus* reared at 8°C had *ca.* 70% less nitrogen and *ca.* 90% less carbon when reared at very low (25 μg C l^{-1}) *versus* excess (500 μg C l^{-1}) food concentration (Campbell *et al.* 2001).

The weights at stage achieved by copepods *in situ* represent an integration of the environmental conditions experienced during life, the length of which will vary with from stage to stage. Thus, for example, with an adequate food supply, an average Stage I *C. finmarchicus* copepodite will be *ca.* 47 days old, if it has experienced a constant temperature of 1°C throughout its development and *ca.* 15 days old, if it has developed at 10°C (Corkett *et al.* 1986). A Stage V, by contrast, will be at least 89 days old, if it has grown up at 1°C and 27 days old or more, if it has developed at 10°C. In addition, many of the adults and Stage V *C. finmarchicus* seen in the surface layers in spring are derived from Stage Vs that have spent the winter in deep water and that may have developed elsewhere. For the other *Calanus* spp. intrinsic growth rates are lower, so that ages at stage will be higher than those of *C. finmarchicus*. In addition, Stages IV, V and adults of both species can overwinter, as can Stage III *C. hyperboreus*. The late stages may thus be 1, 2 or even 3 years old. As well as the changes that individuals might encounter if they stay in a particular area, if they are in an advective system, they may have temperature and feeding histories different from those recorded in the area where they are collected. Thus, individuals within *Calanus* spp. populations at a given station will have experienced a variety of food concentrations and temperatures before they are sampled.

In the AZMP, satellite measurements of sea-surface temperature and chlorophyll are averaged for defined areas (boxes) on the Scotian Shelf over two week periods. Between 1998 and 2001 these show that near-surface temperatures increased from between *ca.* <0 and 3°C in early March to between <2°C and *ca.* 7°C in early May, with the lowest values being recorded over the Eastern Scotian Shelf and the highest values, over Western Bank. In the fall of 1998 they decreased from between 14 °C and 18 °C in early September to between 9 °C and 11 °C in early November. The highest values were on Western Bank, and the lowest on the Western Scotian Shelf in early September and on the Eastern Scotian Shelf in early November. Thus, the temperatures experienced by *Calanus* spp. in samples in the spring would have been lower than those encountered by

copepods caught in the fall. Chlorophyll (phytoplankton food) concentrations measured during spring cruises (April/May, 1998-2001) were generally higher in the spring than those recorded during the fall cruise (October, 1998). According to satellite measurements, however, averages over the early March to early May period were not much higher than averages over the early September to early November period. In addition, in the fall *C. finmarchicus* may supplement their phytoplankton diet with microzooplankton (Ohman and Runge 1994). Thus, the lower weights at stage that were seen for *C. finmarchicus* in the fall were probably mostly due to differences in the temperature history of the animals (Fig. 3, Table 1). The inter-annual differences in weights at stage amongst the four years of spring cruises were probably also linked to differences in temperature and feeding history. For example, in 2000 most *C. finmarchicus* weights at stage were lower than in other springs. In 2000, satellite data shows that most regions of the Scotian Shelf were generally warmer than in the other years and that the spring bloom was of relatively low intensity. The inter-annual differences in spring were tivial, compared with the seasonal difference.

Lower weights at stage were generally seen for *C. glacialis* and *C. hyperboreus* in fall than in spring, but by this time most individuals would have left the surface layers to overwinter, so that only a few stations contributed to the averages (Fig. 3, Table 2). The regional differences in spring (larger in the east than in the west) were also probably related to differences in temperature history, since in the east, and its likely upstream source (the Gulf of St. Lawrence) temperatures were colder than western areas. These differences were judged to be unimportant when selecting values to use to calculate biomass shelf-wide, however. This is because these species/stages occurred at more stations in the east than the west, so that shelf-wide averages were strongly influenced by values from the east, and because they were more abundant in the east, so that the shelf-wide eastern-biased averages were probably appropriate. For *Oithona* the lower weights in fall than in spring may have been related to the stage structures of the populations, although temperature and food effects would still have influenced weights at stage (Table 3). For *Pseudocalanus*, since there was no fall data, the spring values had to be used in calculations of dry weight in both seasons.

The geographical distributions of abundance of the *Calanus* species in spring in 1998-2001 were similar to those reported by Head *et al.* (1999) for 1997. *C. finmarchicus* is generally much more abundant in the west (Browns Bank and Halifax Lines) than in the east (Louisbourg and Cabot Strait Lines). This is because in the west reproduction occurs in March, co-incident with the spring bloom. Thus, large numbers of copepodites of the new generation are present when samples are collected in April and May. In the east, the bloom occurs in April, and in April and May *C. finmarchicus* populations in the east are dominated by overwintered Stage Vs and adults in the process of reproducing. The dry weight biomass of *C. finmarchicus* does not show such a large change from east to west as does abundance, because the Stage Vs and adults are much larger than the young stages (Fig. 5, Table 1).

C. hyperboreus is more abundant in the northeast and Cabot Strait than in the west (Head *et al.* 1999) and because it is much larger than *C. finmarchicus* it dominates the biomass in these regions (Fig. 5). *C. glacialis* is seldom as abundant as either of the other two *Calanus* species and does not generally contribute much to the biomass. *Oithona* is often the most abundant copepod and *Pseudocalanus* concentrations can sometimes be high, but because they are small they generally contribute little to the overall biomass (Table 3, Fig. 5). These species were apparently more important in the spring of 1998 than in other springs, but this might have been because in that year, by mistake, a 100 μm mesh ring net was used to collect the mesozooplankton samples. In this case the young stages of these species, which usually escape capture, would have been caught, adding to the species biomass. On the other hand, the average individual dry weight of *Oithona* in 1998 was only *ca.* 10% lower than the average individual dry weights determined for 1999 and 2000, so the increase in biomass might have been real rather than artifactual.

In spring the slope of the regression between the dry weights calculated for all copepods, using the Harris method, *versus* the dry weights calculated for only the *C* + *O* + *P* groups, was close to one and the intercept value was low (Fig. 6). These features suggest that in spring the *C* + *O* + *P* groups made up a large proportion of the copepod biomass (*e.g.* >70% where the biomass was *ca.* 1 g m^{-2} and >85% where the biomass was *ca.* 3 g m^{-2}). The high r-squared value indicates that using the seasonal average values in the calculations, instead of the station specific values, had no large effect. In fall the higher slope and intercept values for the same relationship, show that the *C* + *O* + *P* groups accounted for a lower proportion of the copepod biomass (*e.g.* <40% where the biomass was *ca.* 1 g m^{-2}). These spring and fall relationships are consistent with observations of copepod community structure between 1998 and 2001 (Head unpubl. data). Similarly, the *C* + *O* + *P* groups accounted for a higher proportion of the total mesozooplankton biomass in spring than in fall. For example, at a total mesozooplankton biomass of *ca.* 3 g m^{-2}, the *C* + *O* + *P* groups accounted for 71% in spring *versus* 53% in fall.

For the AZMP data the relationships between the calculated dry weights of the *C* + *O* + *P* groups and the measured dry and wet weights were not as strong as the one between the dry weights of the *C* + *O* + *P* groups and the sample dry weights calculated by the Harris method (Fig. 7). One factor that might have contributed to this difference is the difference in methodology. In the Harris method, one 10% aliquot is taken from the original samples, and counts and individual dry weights of each group are then determined for volumes of the aliquot that are large enough to give appreciable numbers of counts for each group. For example, for each of the stages of the *Calanus* spp. the analyser aims to count 25, although sometimes this number cannot be achieved. In the AZMP sampling protocol, the dry weight of a sample is determined after an initial split, so that one half of the sampled is dried and weighed and the other half is used for counting. The half that is used for counting is sub-sampled so as to give *ca.* 200 organisms, which are identified and

counted. In practice more organisms (*ca.* 500) are actually counted when mesozooplankton are abundant. The protocol also requires that at least 200 *Calanus* spp. are counted, so that representative patterns of the stage structures are obtained, which may require counting a sub-sample larger than that used for the 200 count. Each splitting or sub-sampling procedure has the potential to introduce errors, and in addition, for any organism (*e.g. Calanus* spp. stage) for which <10 individuals are counted the precision of the count will be $\pm$60%. If the count is <5, the level of precision will be $\pm$100% (Postel *et al.* 2000). Thus, it is likely that several of the *Calanus* spp. individual stage counts will have poor levels of accuracy. In fact at 47% of the stations the ratio of measured dry weight: *C* + *O* + *P* summed dry weight was between 0.75 and 1.25, *i.e.* 1$\pm$50% (data not shown) and at 70% of the stations this ratio was between 0.5 and 2, *i.e.* 1$\pm$100% (Fig. 8). Given the potential for splitting and sub-sampling errors and the lack of precision of the counts, the level of agreement between measurements of dry weight and the *C* + *O* + *P* summed dry weights seems reasonable. By contrast, the Harris procedure is sure to give a higher degree of agreement, because the dry weight of the initial 10% aliquot (and hence of the whole sample) is determined using the counts that were made on that aliquot. Thus, whatever error is introduced during the initial sub-sampling and whatever the level of precision of the counts, the summed dry weight biomass will always be consistent with the counts.

Regardless of the lack of close agreement between the AZMP measured dry weights and those estimated by summing the dry weights of *Calanus* spp., *Oithona* and *Pseudocalanus*, this method is still useful for investigating some features of the mesozooplankton community. Abundance values, as are reported in the AZMP, are important, but seeing which species dominate the biomass is also important: abundance and biomass measurements give rather different distribution patterns on the Scotian Shelf (*c.f.* Head *et al.* 1999 and Fig. 5). Also, in studies investigating larval and juvenile fish feeding, it may also be important to know the distribution of biomass amongst different stages and sizes of *Calanus* spp. (*e.g.* Munk 1997). In order to use this method, however, the individual dry weights to be used must be appropriate. The values reported here for the Scotian Shelf in spring and fall are probably quite reliable, because they have been derived from relatively large datasets, but the values for the Newfoundland Shelf, the Labrador Shelf (Hamilton Bank) and Labrador Slope waters were derived from far fewer measurements (Tables 4-7). These latter individual weights were sometimes rather different from the Scotian Shelf values. For example, individual *Pseudocalanus* were 3 times larger in Labrador Shelf and Slope waters than on the Scotian Shelf in spring, and in these same areas late stage *Calanus* spp. were up to 30% larger in summer than they were in spring on the Scotian Shelf. Additional measurements should probably be made in these areas, to give more robust measurements of individual dry weight values, and elsewhere (*e.g.* Gulf of St. Lawrence,) to provide values appropriate for those regions.

Summary

Individual weights at stage for *Calanus finmarchicus*, *C. glacialis and C. hyperboreus* on the Scotian Shelf are lower in the fall than in spring and they vary between years in spring, because of differences in temperature and food conditions. Average individual weights of groups of mixed stages of *Oithona* spp. are lower in fall than in spring, probably because of differences in both environmental conditions and population stage structure.

Spring or fall individual dry weights of the stages of the three *Calanus* species and of the mixed stages of *Oithona* and *Pseudocalanus* (*C* + *O* + *P*) were used together with abundance data to calculate the combined dry weight of these groups for samples collected on the Scotian Shelf. These samples had been analysed in one of two ways. For one set (the Head and Harris samples) one aliquot was taken from the original samples, which was used both for counting and to estimate the total mesozooplankton dry weight. For the other set (the AZMP samples) the total mesozooplankton dry weight was measured on one half of the original sample and the other half was used for counting. The combined dry weight of the *C* + *O* + *P* groups showed strong linear relationships with the total mesozooplankton biomass for the Head and Harris samples in both spring and fall. The same relationships were not as close for the AZMP samples. It is possible that splitting and sub-sampling procedures, and imprecision in counting, may have contributed to the absence of a strong relationship between *C* + *O* + *P* dry weight and measured dry weight for the AZMP samples.

For the Head and Harris samples, the relationship between dry weight and total mesozooplankton dry weight showed that in spring the *C* + *O* + *P* groups account for a large proportion of the total mesozooplankton biomass on the Scotian Shelf, although the very abundant small copepods *Oithona* spp. and *Pseudocalanus* spp. actually make relatively small contributions. In the fall the contribution of the *C* + *O* + *P* to the total biomass is reduced, but it is still important.

The combination of appropriate individual dry weights with abundance data, in the AZMP, will allow for the estimation of the biomass of each of these species, and a better understanding of zooplankton community structure in the region's ecosystems.

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http://www.meds-sdmm.dfo-mpo.gc.ca/zmp/Plankton/zoo/zoo_e.html

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Table 1. Average weights at stage (μg) for *Calanus finmarchicus* on the Scotian Shelf (± S.D.). N is the number of stations contributing to the average.

	Females	Males	Stage V	Stage IV	Stage III	Stage II	Stage I
Spring							
1998	306.44	321.46	235.56	95.41	29.84	9.85	3.66
	(±64.78)	(±82.53)	(±58.17)	(±19.53)	(±7.50)	(±2.73)	(±0.90)
1999	297.48	276.41	230.34	83.44	28.25	10.42	3.66
	(±48.93)	(±70.76)	(±42.43)	(±24.17)	(±10.08)	(±4.52)	(±0.91)
2000	272.14	277.73	204.36	81.33	22.88	8.08	3.44
	(±45.61)	(±51.39)	(±41.54)	(±20.68)	(±6.40)	(±2.62)	(±0.87)
2001	351.38	308.22	268.45	90.48	26.39	9.04	3.48
	(±44.42)	(±71.18)	(±45.35)	(±20.50)	(±6.88)	(±2.31)	(±0.77)
All Springs							
Average	308.50	295.25	234.96	87.40	26.39	9.16	3.54
S.D.	(±59.70)	(±70.76)	(±53.36)	(±21.80)	(±8.01)	(±3.12)	(±0.86)
N	195	149	200	192	178	186	185
Fall 1998							
Average	214.35	198.55	154.44	51.32	17.91	7.44	2.82
S.D.	(±26.52)	(±47.33)	(±47.43)	(±13.50)	(±8.76)	(±2.05)	(±0.44)
N	28	20	35	33	30	22	12

Table 2. Average weights at stage (μg) for *Calanus glacialis* and *C. hyperboreus* on the Scotian Shelf (±S.D.). N is the number of stations contributing to the average.

	Females	Males	Stage V	Stage IV	Stage III	Stage II	Stage I
C. glacialis - All springs							
Average	795.53	582.50	558.86	203.89	57.45	19.10	6.57
S.D.	(±184.45)	(±149.56)	(±151.11)	(±63.46)	(±23.56)	(±7.76)	(±2.11)
N	66	4	119	130	119	124	128
C. glacialis - Fall 1998							
Average	478.67	N.D.	469.64	250.67	N.D.	N.D.	N.D.
S.D.	(±114.09)		(±7.64)	(±55.27)			
N	3		2	5			
C. hyperboreus - All springs							
Average	2761.47	N.D.	1144.96	355.87	129.09	41.46	11.29
S.D.	(±700.61)		(±409.41)	(±102.49)	(±49.94)	(±17.33)	(±3.33)
N	69		143	175	182	142	108
C. hyperboreus - Fall 1998							
Average	N.D.	N.D.	N.D.	252.61	75.00	N.D.	N.D.
S.D.				(±87.08)	(±15.00)		
N				4	2		

Table 3. Average individual dry weights (μg) for mixed stages of *Oithona* and *Pseudocalanus* (±S.D.). N is the number of stations contributing to the average.

All springs	(1998-2000)	(1995-1996)
Average	1.47	6.75
S.D.	(±0.34)	(±2.33)
N	143	41
Fall	1998	
Average	0.99	N.D.
S.D.	(±0.27)	
N	43	

Table 4. Average weights at stage (μg) for *C. finmarchicus* on the Scotian Shelf (spring) and the Newfoundland Shelf, Hamilton Bank and the adjacent Labrador Slope waters (spring and summer). (±S.D.). N is the number of stations contributing to the average.

	Females	Males	Stage V	Stage IV	Stage III	Stage II	Stage I
Scotian Shelf - Spring							
Average	308.50	295.25	234.96	87.40	26.39	9.16	3.54
S.D.	(±59.70)	(±70.76)	(±53.36)	(±21.80)	(±8.01)	(±3.12)	(±0.86)
N	195	149	200	192	178	186	185
Newfoundland Shelf – Spring							
Average	347.88	256.89	266.94	106.79	32.34	10.54	3.73
S.D.	(±41.81)	(±26.71)	(±68.53)	(±36.35)	(±2.82)	(±1.98)	(±1.28)
N	11	10	11	11	5	6	9
Hamilton Bank – Spring							
Average	322.52	235.42	178.82	94.44	21.75	7.42	3.03
S.D.	(±40.50)	(±68.89)	(±46.27)	(±17.33)	(±7.87)	(±1.33)	(±0.63)
N	10	7	10	9	5	3	2
Labrador Slope - Spring							
Average	369.83	330.66	227.03	112.58	31.76	9.53	4.19
S.D.	(±48.72)	(±92.16)	(±50.52)	(±29.73)	(±3.35)	(±0.68)	(±1.25)
N	7	7	7	7	4	4	6
Newfoundland Shelf – Summer							
Average	420.12	N.D.	283.71	69.90	20.70	6.87	2.28
S.D.	(±39.07)		(±91.40)	(±12.90)	(±7.54)	(±3.47)	(±0.46)
N	9		6	9	8	9	9
Hamilton Bank – Summer							
Average	418.83	259.32	313.89	102.43	32.61	9.51	3.28
S.D.	(±41.60)	(±73.42)	(±44.36)	(±15.40)	(±7.67)	(±2.10)	(±0.71)
N	17	5	16	16	16	17	17
Labrador Slope – Summer							
Average	422.65	448.88	310.41	90.55	23.80	8.46	2.66
S.D.	(±27.21)	(±63.73)	(±17.49)	(±8.50)	(±7.79)	(±1.53)	(±0.91)
N	9	8	9	9	7	5	4

Table 5. Average weights at stage (μg) for *C. glacialis* on the Scotian Shelf (spring) and the Newfoundland Shelf, Hamilton Bank and the adjacent Labrador Slope waters (spring and summer). (±S.D.). N is the number of stations contributing to the average.

	Females	Males	Stage V	Stage IV	Stage III	Stage II	Stage I
Scotian Shelf - Spring							
Average	795.53	582.50	558.86	203.89	57.45	19.10	6.57
S.D.	(±184.45)	(±149.56)	(±151.11)	(±63.46)	(±23.56)	(±7.76)	(±2.11)
N	66	4	119	130	119	124	128
Newfoundland Shelf – Spring							
Average	763.67	N.D.	664.98	209.01	52.56	19.72	6.5
S.D.	(±321.09)		(±127.80)	(±39.31)	(±13.79)	(±4.12)	(±0.80)
N	8		7	9	6	9	9
Hamilton Bank – Spring							
Average	770.02	596.67	536.30	198.82	59.03	18.71	6.14
S.D.	(±137.86)	(±135.73)	(±96.12)	(±47.42)	(±29.85)	(±12.19)	(±1.85)
N	10	3	10	10	5	6	8
Labrador Slope – Spring							
Average	912.27	N.D.	561.52	183.04	67.00	N.D.	7.3
S.D.	(±315.57)		(±148.84)	(±56.67)	(±17.00)		(±1.78)
N	6		5	4	2		3
Newfoundland Shelf – Summer							
Average	1116.74	N.D.	668.08	171.64	41.69	11.93	4.98
S.D.	(±321.09)		(±127.80)	(±39.31)	(±13.79)	(±4.12)	(±0.80)
N	8		7	9	6	9	9
Hamilton Bank – Summer							
Average	1044.31	585.00	770.69	245.79	69.91	19.13	6.29
S.D.	(±169.72)		(±117.36)	(±66.63)	(±17.82)	(±5.73)	(±1.70)
N	16	1	17	13	16	14	17
Labrador Slope – Summer							
Average	N.D.	N.D.	736.83	N.D.	N.D.	10.00	N.D.
S.D.			(±186.06)				
N			6			1	

Table 6. Average weights at stage (μg) for *C. hyperboreus* on the Scotian Shelf (spring) and the Newfoundland Shelf, Hamilton Bank and the adjacent Labrador Slope waters (spring and summer). (±S.D.). N is the number of stations contributing to the average.

	Females	Males	Stage V	Stage IV	Stage III	Stage II	Stage I
Scotian Shelf - Spring							
Average	2761.47	N.D.	1144.96	355.87	129.09	41.46	11.29
S.D.	(±700.61)		(±409.41)	(±102.49)	(±49.94)	(±17.33)	(±3.33)
N	69		143	175	182	142	108
Newfondland Shelf – Spring							
Average	3845.11	N.D.	1759.46	513.55	91.17	32.32	9.71
S.D.	(±1448.46)		(±633.04)	(±263.08)	(±37.08)	(±7.30)	(±2.06)
N	10		11	9	9	10	10
Hamilton Bank – Spring							
Average	2627.65	N.D.	1275.41	302.10	106.18	32.59	9.31
S.D.	(±663.73)		(±263.27)	(±125.64)	(±56.92)	(±23.76)	(±3.60)
N	7		10	8	10	10	10
Labrador Slope – Spring							
Average	3084.00	N.D.	1401.28	405.68	130.64	26.82	10.73
S.D.	(±816.34)		(±468.15)	(±137.16)	(±28.85)	(±5.96)	(±3.48)
N	6		7	7	5	6	5
Newfoundland Shelf – Summer							
Average	N.D.	N.D.	1858.67	466.62	104.23	43.38	N.D.
S.D.			(±188.48)	(±84.97)	(±54.88)	(±17.17)	
N			3	9	7	4	
Hamilton Bank – Summer							
Average	4866.00	N.D.	1789.92	506.40	192.12	49.41	8.85
S.D.	(±866.25)		(±734.74)	(±123.45)	(±56.15)	(±21.14)	(±1.61)
N	5		11	17	16	12	9
Labrador Slope – Summer							
Average	N.D.	N.D.	1647.22	443.39	114.06	30.00	N.D.
S.D.			(±233.03)	(±59.47)	(±19.44)		
N			6	9	8	1	

Table 7. Average individual weights (μg) of mixed stages of *Oithona* and *Pseudocalanus* on the Scotian Shelf (spring) and the Newfoundland Shelf, Hamilton Bank and the adjacent Labrador Slope waters (spring and summer). (±S.D.). N is the number of stations contributing to the average.

	Oithona	*Pseudocalanus*
All springs	(1998-2000)	(1995-1996)
Average	1.47	6.75
S.D.	(±0.34)	(±2.33)
N	143	41
Newfoundland Shelf - Spring		
Average	1.32	N.D.
S.D.	(±0.25)	
N	11	
Hamilton Bank – Spring		
Average	1.24	22.66
S.D.	(±0.18)	(±2.09)
N	10	4
Labrador Slope – Spring		
Average	1.95	21.69
S.D.	(±0.85)	(±4.21)
N	7	3
Newfoundland Shelf – Summer		
Average	1.36	6.62
S.D.	(±0.18)	(±3.76)
N	9	9
Hamilton Bank – Summer		
Average	1.65	9.00
S.D.	(±0.38)	(±1.5)
N	17	3
Labrador Slope – Summer		
Average	1.23	N.D.
S.D.	(±0.28)	
N	8	

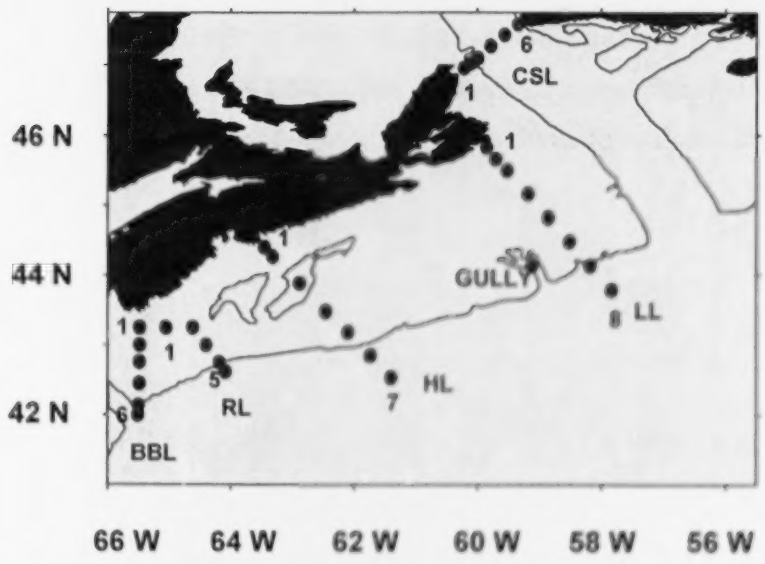


Fig. 1. Stations sampled on a regular basis on the Scotian Shelf during spring and fall 1998-2001. BBL, Browns Bank; RL, Roseway Line; HL, Halifax Line; LL, Louisbourg Line; CSL, Cabot Strait Line.

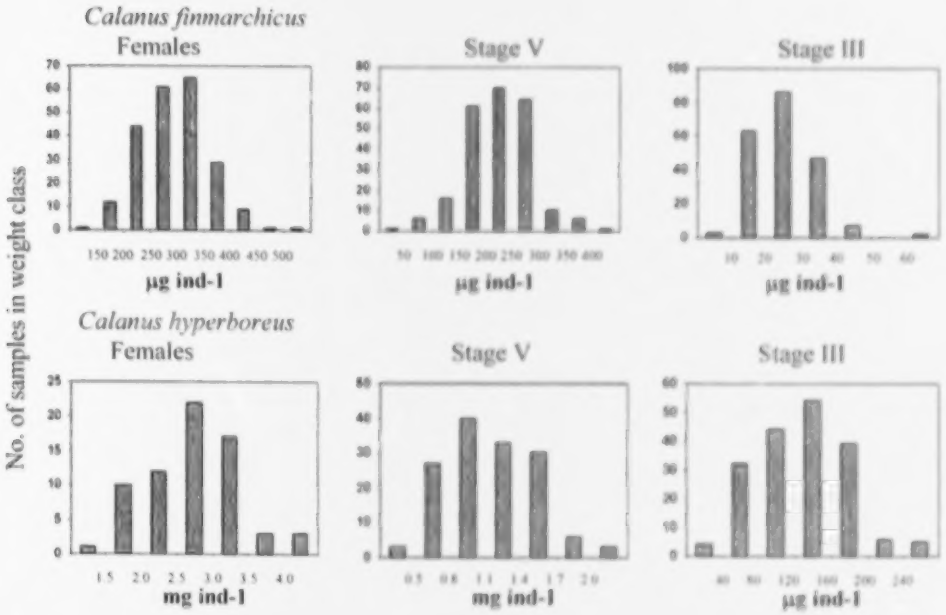


Fig. 2. Weight-frequency distributions of female, stage V and Stage III of *Calanus finmarchicus* and *Calanus hyperboreus* from the Scotian Shelf (spring 1998-2001, fall 1998)

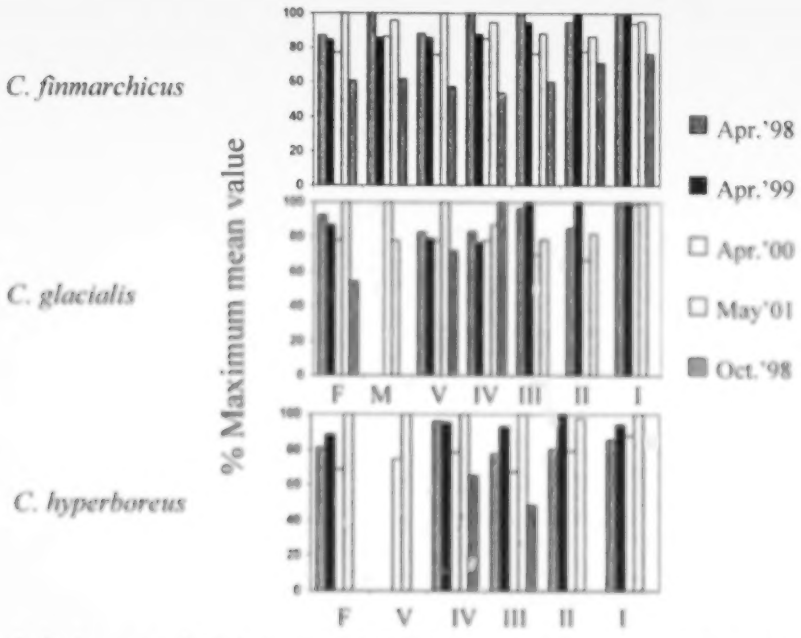


Fig. 3. Cruise average individual weights for *Calanus* spp. on the Scotian Shelf. For each stage the maximum observed value was set at 100%. The values for the other cruises were then calculated as a percentage of the maximum. Some groups were not always present.

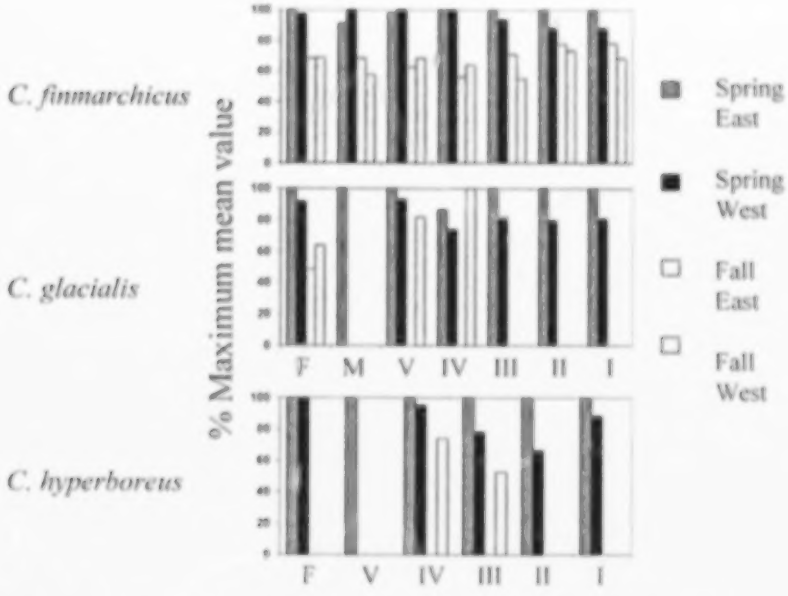


Fig. 4. Average weights at stage for spring and fall cruises in eastern (Cabot Strait and Louisbourg Lines) and western (Halifax and Browns Bank Lines) regions of the Scotian Shelf. For each stage the maximum observed value was set at 100%. The values for the other seasons/regions were then calculated as a percentage of the maximum. Some groups were not always present.

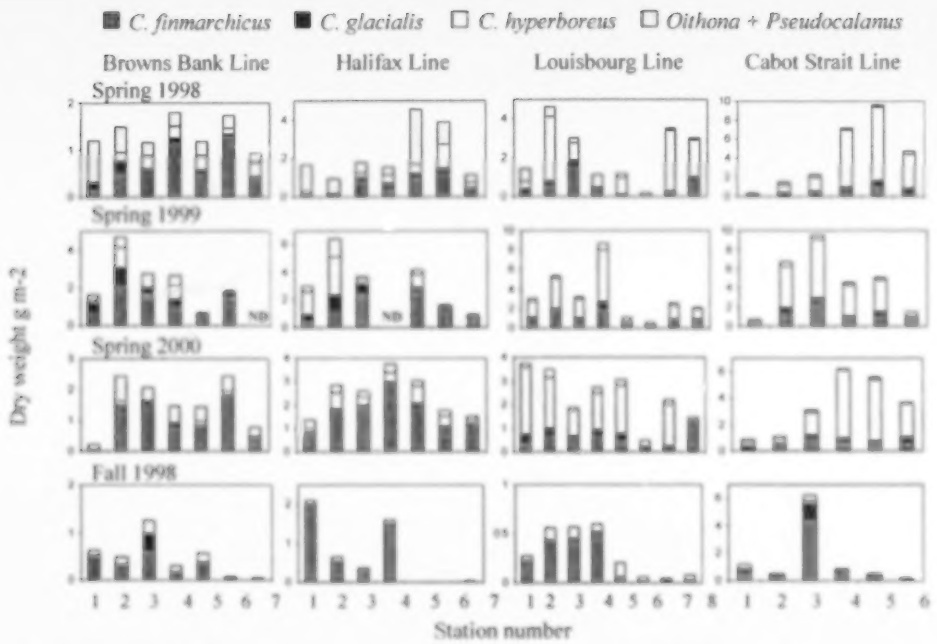


Fig. 5. Dry weights of *Calanus* spp. and *Oithona* + *Pseudocalanus* spp. on the Scotian Shelf calculated using the seasonal average individual dry weights and abundances.

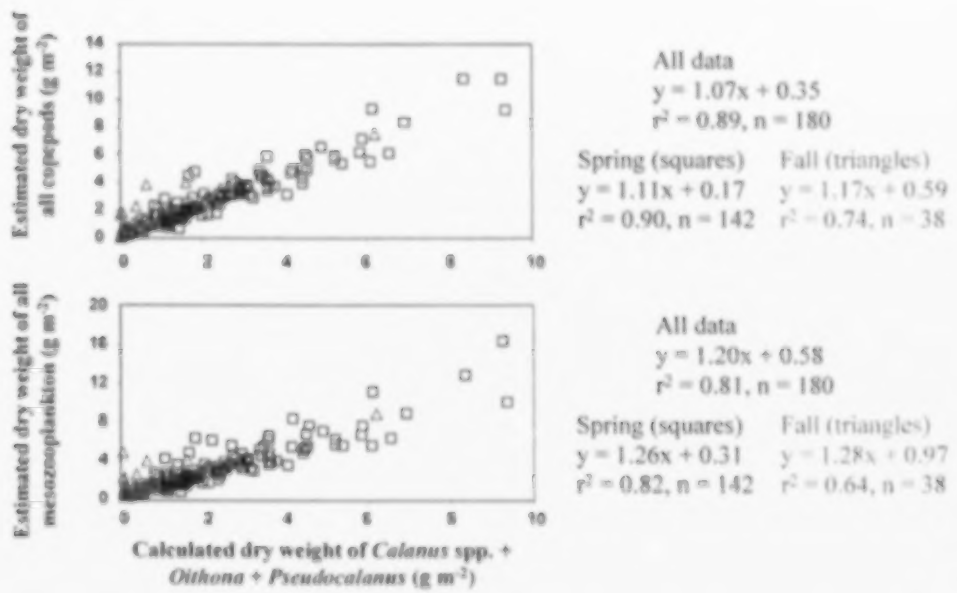
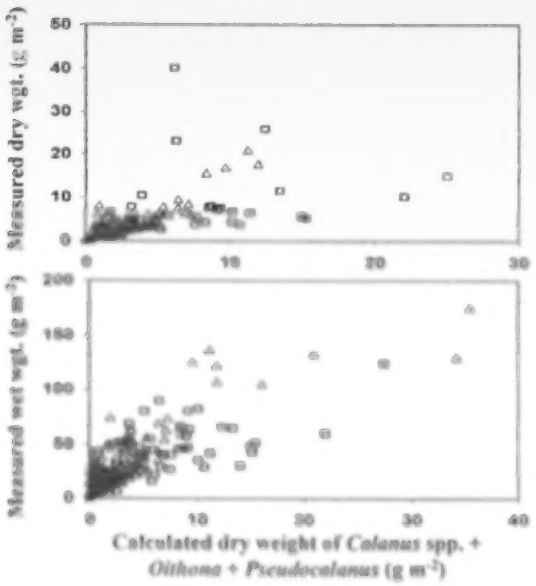

Estimated dry weight of all copepods (g m-2)
All data
y = 1.07x + 0.35
r2 = 0.89, n = 180
Spring (squares)
y = 1.11x + 0.17
r2 = 0.90, n = 142
Fall (triangles)
y = 1.17x + 0.59
r2 = 0.74, n = 38
Estimated dry weight of all mesozooplankton (g m-2)
All data
y = 1.20x + 0.58
r2 = 0.81, n = 180
Spring (squares)
y = 1.26x + 0.31
r2 = 0.82, n = 142
Fall (triangles)
y = 1.28x + 0.97
r2 = 0.64, n = 38
Calculated dry weight of Calanus spp. + Oithona + Pseudocalanus (g m-2)

Fig. 6. Linear regressions of the Head and Harris estimates of the dry weights of all copepods (upper panel) and all mesozooplankton (lower panel) versus the summed calculated dry weights of *Calanus* + *Oithona* + *Pseudocalanus* (*C* + *O* + *P*).



All data
$y = 0.72x + 1.79$
$r^2 = 0.32$, n = 144

Spring (squares)	Fall (triangles)
$y = 0.57x + 2.22$	$y = 1.36x + 0.50$
$r^2 = 0.21$, n = 72	$r^2 = 0.77$, n = 72

All data
$y = 4.02x + 17.75$
$r^2 = 0.39$, n = 224

Spring (squares)	Fall (triangles)
$y = 3.18x + 16.53$	$y = 4.85x + 19.43$
$r^2 = 0.46$, n = 97	$r^2 = 0.42$, n = 127

Fig. 7. Linear regressions of dry and wet weights, measured according to the AZMP protocols versus the summed calculated dry weights of the stages of *C* + *O* + *P*.

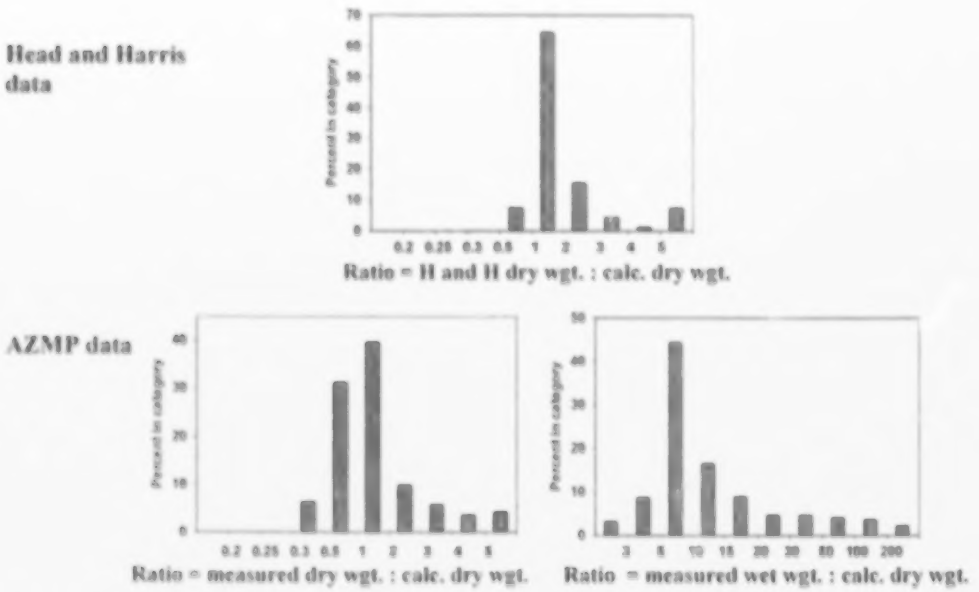

Head and Harris data
Percent in category
Ratio = H and H dry wgt. : calc. dry wgt.
AZMP data
Ratio = measured dry wgt. : calc. dry wgt.
Ratio = measured wet wgt. : calc. dry wgt.

Fig. 8. Frequency distributions of the ratios of the Head and Harris mesozooplankton: *C* + *O* + *P* dry weights (upper panel), the AZMP measured: *C* + *O* + *P* dry weights (lower left panel) and measured wet weight: *C* + *O* + *P* dry weights (lower right panel).

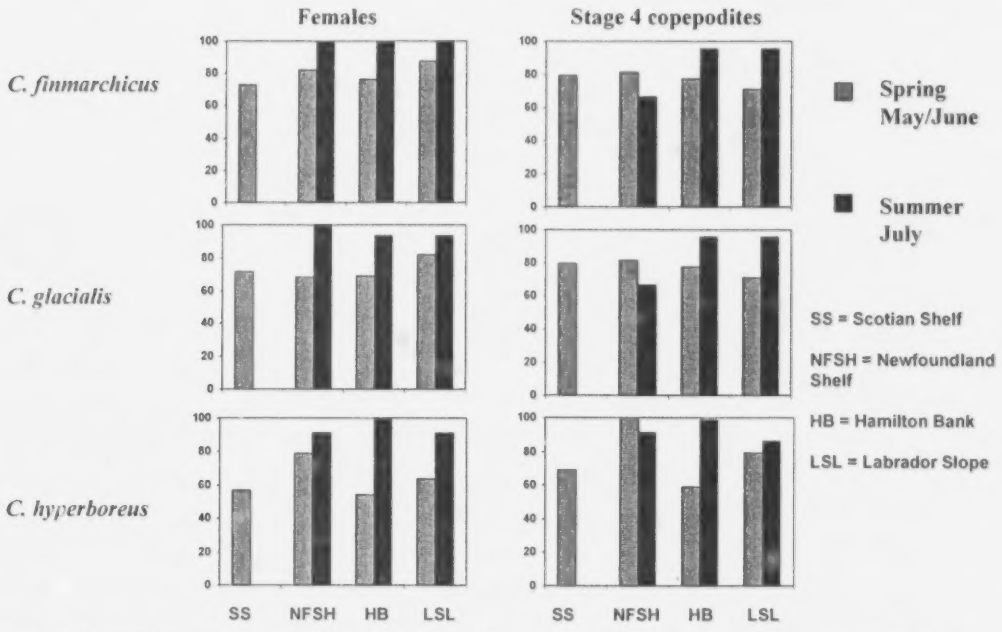


Fig. 9. Comparisons of average individual dry weights of female and stage IV *Calanus* spp. from the Scotian Shelf in spring and the Newfoundland Shelf, Hamilton Bank and Labrador Slope waters in spring and summer. For each stage the maximum observed value was set at 100%. The values for the other seasons/regions were then calculated as a percentage of the maximum.